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Herbivory and seedling establishment in Pyrenean forests: influence of micro- and meso-habitat factors on browsing pressure

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ABSTRACT

Browsing damage is among the most determinant factors that limit the establishment of tree seedlings in forests. In some areas, this process leads to massive mortalities that can reduce or even completely prevent the regeneration of some tree species. Mediterranean mountain forests have undergone during the last decades important changes in land-uses that have significantly altered the type and abundance of herbivore populations. In this study we assessed the impact of current grazing conditions in forest regeneration using a set of experimental plantations established in the Eastern Pyrenees in areas visited by domestic livestock (cattle and horses) and wild ungulates (mainly roe deer and chamois). We analyzed during 4 years the role of seedling species and size, mesohabitat (elevation and type of forest cover) and microhabitat (herbaceous cover, distance to shrub, and light availability) on the browsing-induced mortality of more than 500 seedlings of *Pinus sylvestris*, *Pinus uncinata*, *Betula pendula* and *Abies alba*, the most common tree species in the study area. Browsing-induced mortality for the three conifer species was much lower (<15%) than the one observed for *B. pendula* (>40%) and depended on both microhabitat – mainly on the distance to protective elements such as shrubs; and mesohabitat, with an interaction between the elevational belt (site) and the type of forest cover (gaps *vs.* understory). In the subalpine belt, browsing on *A. alba* and *P. uncinata* was higher during summer at plots located in the forest understory whereas, during winter, it was higher at plots located in gaps. The study shows that both mesohabitat and microhabitat can exert an effect on the patterns of plant damage by herbivores, providing useful information to adapt forest management in areas particularly exposed to them.

Keywords: Browsing, mortality, ungulates, livestock, seedlings, Pyrenees

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1. INTRODUCTION

Forests regeneration is limited by several environmental constraints. Among them, browsing by large herbivores is often one of the most determinant factors, particularly in mountain areas, where tree establishment and growth are already constrained by unfavorable environmental conditions (Ameztegui and Coll, 2013). In the last decades, many European mountains have undergone major changes in the type, abundance and behavior of their main herbivore populations – including both wild and domestic animals – as a consequence of the profound socioeconomic changes that have affected these systems (Casals et al., 2009). For instance, the Pyrenees have recently changed from a transhumant system – in which sheep for wool production were favored against cattle, and there was an extensive utilization of most available food sources – to a system in which the overall livestock pressure is notably lower, and beef cattle and breeding mares have partially substituted sheep herds (Garcia-Ruiz and Lasanta, 1990; Lasanta, 1990). Under this new organization of the landscape, intensive grazing pressures concentrate in very limited areas (mainly subalpine pastures), whereas many pastures that were suitable for sheep are now unused (Balcells, 1983). The abandonment of these lands together with a reduction of logging pressure on forests have led to important forest expansion processes and to a generalized increase in canopy closure (Ameztegui et al., 2010; Poyatos et al., 2003). Wild ungulates such as roe deer (*Capreolus capreolus*) or chamois (*Rupicapra pyrenaica*) find in these dense forests a suitable habitat and have sharply increased their populations in the last decades (Apollonio et al., 2010; Putman et al., 2011).

The progressive increase in ungulate populations during the last decades has already caused some concern due to the consequences it could entail for the regeneration of European temperate forests (see, for example Motta 1996, Putman 1996 or Bugmann and Weisberg 2003). At high stocking densities, herbivory can even completely prevent regeneration of some species and lead to a reduction of plant species diversity (Ammer, 1996; Danell, 2003; Reimoser, 1996).

Changes in herbivore populations – both in livestock and wildlife – can severely affect the patterns of seedling consumption and lead to shifts in forest composition on the mid-term (Gill, 1992; Motta, 1996; Senn and Suter, 2003), and patterns of seedling predation by large herbivores can themselves be affected by other environmental factors (Weisberg and Bugmann, 2003). Available tree species, forest structure, type of habitat, period of grazing or the amount of alternative food sources, among others, affect how frequently and intensely herbivores browse young trees (Liss, 1988; Mayer, 2005a; Mayer et al., 2003; Reimoser, 1996). Yet, we are still far from a complete understanding of the combined effect that these environmental factors can exert on browsing patterns (Bergström and Edenius, 2003; Kräuchi et al., 2000).

In this study, we aim at shedding some light on the role that the complex ungulate-habitat interactions play on the dynamics of mountain forests. For this purpose, we planted seedlings of the main tree species in the Eastern Pyrenees in an area grazed both by livestock and wild ungulates, and under contrasting environmental conditions. By planting even-aged seedlings in areas with non-modified browsing conditions, we wanted to assess the effect of specific seedling selection by herbivores (Kupferschmid et al., 2014). Mortality of seedlings due to browsing, although often non-visible, can be more determinant on forest dynamics than mortality of saplings, but the later has been more studied because the damages are more evident and easier to determine (Reimoser, 2003; Senn and Suter, 2003). More specifically, the study aimed to (i) assess the impact of current grazing conditions (both of livestock and wild ungulates) in forest establishment; (ii) detect if some tree species were preferred by herbivores over others; (iii) determine how variations in meso-habitat (elevation and type of forest cover) and microhabitat (herbaceous cover, distance to shrub, light availability) may engender different patterns of plant consumption by herbivores; and (iv) discuss the potential implications of the observed patterns for forest dynamics. We expect a highly selective predation on silver fir and birch, which can prevent the diversification of pine forest described elsewhere in the absence of

92 management (Navarro-González et al., 2013). At the meso-habitat scale, we expect livestock to
93 cause less damage than wild ungulates at forest gaps; whereas at the micro-habitat scale, the
94 predation rate is likely to be positively affected by herb abundance and negatively by shrubs.

95 **2. MATERIAL AND METHODS**

96 **2.1. Study area and species**

97 We conducted the experiment at two sites with different elevations in the northern slopes of the
98 Serra del Cadí, a Pyrenean mountain range in the Cadí-Moixeró Natural Park (42º17'N;
99 1º42'E). The Sant Romà site corresponds to a montane pine forest located at 1500 m a. s. l.
100 (near the *P. sylvestris – P. uncinata* transition zone), while the Prat d'Aguiló site is a typical
101 subalpine forest located close to the optimum elevational distribution for *P. uncinata* (around
102 2000 m a. s. l.; Figure 1). The forest in Sant Romà was dominated by *P. sylvestris,* with some *P.*
103 *uncinata* and *B. pendula* individuals, and the main species in the understory were common box
104 (*Buxus sempervirens* L.) and common juniper (*Juniperus communis* L.). Prat d'Aguiló forests
105 were dominated by *P. uncinata* and the shrub layer was almost exclusively composed by *J.*
106 *communis*.

107 Despite being a protected area, herds of cows and horses graze every summer in both sites
108 (Table 1), since the authorities have promoted animal husbandry as a major source of income
109 for local communities. The area also hosts important populations of chamois (*Rupicapra*
110 *pyrenaica*), and roe deer (*Capreolus capreolus)*, with a lower presence of wild boar (*Sus*
111 *scrofa*), and red deer (*Cervus elaphus*).

112 We used for this study the four most common tree species in the study area: Scots pine (*Pinus*
113 *sylvestris* L.), mountain pine (*Pinus uncinata* Ram. ex DC), silver fir (*Abies alba* Mill.) and
114 silver birch (*Betula pendula* Roth). These species have different ecological requirements in
115 terms of tolerance to shade, drought and cold temperatures (see Ameztegui and Coll 2013 for

116 further details) but they can coexist between 1600 and 2000 m a. s. l., where they constitute the
117 montane-subalpine ecotone.

118 **2.2. Experimental design**

119 A total of 1152 seedlings of the study species were planted in the early summer of 2008.
120 Seedlings were distributed along 24 plots (12 at the montane site and 12 at the subalpine),
121 located at less than 300 m from grasslands highly frequented by livestock (Figure 1). At each
122 site, half of the plots (6) were established in the forest understory and the other half (6) in
123 naturally occurring gaps, whose size ranged between 150 and 350 m^2. Each plot contained 48
124 seedlings (12 per species) randomly distributed in a grid pattern, and seedlings were planted at
125 least one meter one from another to avoid above- and belowground interaction. All the seedlings
126 were two years old at the moment of plantation, and had been grown in a local nursery (Forestal
127 Catalana, Pobla de Lillet, Spain) from seeds collected in neighboring forests, i.e., seed source,
128 nursery, and plantation area were all inside the same provenance region (Alía et al., 2005). To
129 ensure enough seedling survival to assess the role of climate and microsite on seedling
130 performance (see Ameztegui and Coll, 2013), half of the seedlings in each plot were protected
131 from browsing with an individual protector (90 cm height and 33 cm of diameter) with a mesh
132 net of 20 x 20 mm (Nortène, Lille, France). The remaining half (n=576) was left unprotected
133 and constitute the sample of this study, since they allowed us to assess for the effects of
134 browsing by large herbivores on seedling performance.

135 **2.3. Presence of herbivores in the study area**

136 Both sites are highly frequented by livestock during summer, when a total of 95 cows and 60
137 mares – i.e. 124 adult livestock units – take advantage of the pastures located close to the
138 experimental sites under a free-range, extensive system. During summer, the high presence of
139 domestic cattle forces most wildlife to take refuge in the rocky areas located above the main
140 grazing areas. On the contrary, wild ungulates are the unique large herbivores in the study area

during winter, when livestock is stabled in the valley. Although there are no recent censuses of wild ungulates in the study area, the populations of roe deer, chamois, red deer and wild boar have increased in the last decades (DGMNB, 2014). The study area is located inside the Cadí National Game Reserve, created in 1966 to protect a population of 78 specimens of chamois. The last census of this species performed in 1999 revealed that the population had risen up to 2,551 individuals (5. 4 chamois · km^{-2}).

2.4. Seedling monitoring and characterization of the habitat

Individual seedling damage and mortality were monitored at the beginning and at the end of each growing season during four years since the moment of plantation. The likely cause of damage or death was recorded when apparent as whether due to (i) herbivores (browsing, trampling or other type of physical damage caused by browsers); (ii) lack of adaptation (i.e., showing symptoms of drought or cold sensitivity such as partially or totally brown leaves); and (iii) random causes (tree or stone falls, downhill creep). We did not find plants severely affected by other biotic agents such as insects or fungi. We defined browsing-induced mortality as the proportion of the seedlings that died within the study period, and for which the apparent cause of death were herbivores. We also monitored the recovery of those browsed seedlings that did not die immediately, and we computed lethality as the proportion of seedlings that, having been browsed, ended up dying. We described the environment in which seedlings were growing at two spatial scales: mesohabitat (at the plot level) and microhabitat (at the individual level). Mesohabitat was described through the elevational stages of vegetation (montane vs. subalpine) and the type of forest cover (understory vs. gap). On the other hand, microhabitat was characterized by light availability, percentage of herbaceous cover and distance to the nearest shrub, measured for every planted seedling (Table 1). Light availability was determined, for each seedling, as percentage of the above canopy photosynthetic photon flux density (%PPFD). Measurements were taken using two Li-190SA quantum sensors (LI-COR, Lincoln, NE, USA)

in paired mode, i.e. one of the sensors was placed at the top of each seedling and the other in an adjacent open area (following Parent and Messier 1996). The percentage of herbaceous cover surrounding each plant was visually estimated – to the nearest 5% – by placing an 80 x 80 cm reticulated grid centered on each seedling. Distance from each seedling to the nearest shrub – defined as a woody plant with multiple stems arising from the base – was measured with a tape meter.

2.5. Data analyses

For each species, survival function curves were constructed for the unprotected plants (n = 576), using Kaplan–Meier estimates based on data of browsed-induced mortality along the study period. This kind of analyses allow for assessment of the occurrence of an event (in this case, the mortality due to browsing) while taking into account censored data, i.e. observations for which the information about their survival time is incomplete, whether because they are alive at the end of the observation period or because they quit the study before completion (in this case, seedlings whose mortality was not related to browsing). Mantel–Cox log-rank tests were used to determine significant differences in the survival curves between sites (montane *vs*. subalpine) and types of forest cover (gap *vs*. understory).

To assess the effect of meso- and micro-habitat factors on seedling mortality we computed browsing-induced probability of mortality for every species and plot, using the value of the Kaplan-Meier estimators at the end of the study period. We assessed the effect of mesohabitat factors (elevation and forest cover) on browsing mortality via a split-plot ANOVA in which elevation was considered as the main factor and type of forest cover as the sub-plot factor. Exploratory analyses showed that the effect of browsing on seedling mortality varied with species, elevation and forest cover, and we found a significant three-way interaction. Hence, to facilitate interpretation of the results, they are presented using within-species analyses. We split the data into summer and winter seasons to test for potential effects of the main type of browser

(wild ungulates *vs.* livestock) on the patterns of mortality. One-sample t-tests with Bonferroni corrections were performed to test significant deviations from zero of the mortality values.

To test the effect of micro-habitat on the browsing-induced mortality, each microsite explanatory variable (light availability, herbaceous cover and distance to shrubs) was analyzed separately for each species using logistic models:

$$y = \frac{e^z}{1 + e^z}$$

where y is the probability of browsing-induced mortality for an individual sapling, and z a parameter to estimate. To allow for non-linear relationships between the response and independent variable, we tested linear, power and exponential formulations for z. The procedure used to test the role of an independent variable on seedling performance was the same for all the models, and was based on a likelihood approach. The best of the 3 formulations (linear, power and exponential) was compared to a null model using ΔAICc, the difference in corrected Akaike Information Criterion (Burnham and Anderson, 2002). The maximum likelihood parameter values were estimated using simulated annealing, and asymptotic 2-unit support intervals were used to assess the strength of evidence for individual parameter estimates (Goffe et al., 1994). The squared correlation coefficient (R^2) of the regression between observed and predicted values was used as a measure of the goodness-of-fit of each model. All analyses were performed using R 2.12.2 software (R Development Core Team, 2010) and the 'likelihood' and 'survival' packages for R.

209 ## 3. RESULTS

210 ### 3.1. General patterns of browsing-induced seedling damage and mortality

211 After 40 months of observation, browsing emerged as the most important cause of mortality for
212 *B. pendula* – 40% of the seedlings of this species were browsed to death during the study period
213 –, but mortality due to browsing never exceeded 15% for the three conifer species (Table 2). No
214 significant differences in survival curves were observed between sites, i.e. browsing-induced
215 mortality was similar at both elevations for each species (Figure 2). Overall lethality (i.e., the
216 proportion of browsed trees that ended up dying) was high (over 70%) but there were some
217 differences across species, with the three conifer species (*A. alba*, *P. sylvestris* and *P. uncinata*)
218 showing higher lethality values (average values ranging from 67 to 81%) than birch, the only
219 study species with sprouting ability (Table 3).

220 ### 3.2. Effect of mesohabitat on seasonal patterns of browsing-induced mortality

221 *B. pendula* seedlings were heavily browsed – both during winter and summer – at all the tested
222 mesohabitats and comparable mortality rates were found across elevations and types of forest
223 cover (Figure 3). In contrast, the mortality rate due to browsing showed for *A. alba* and *P.*
224 *uncinata* a marked seasonal effect, with an interaction between season and elevation. During
225 winter, browsing-induced mortality for these two species was observed on both elevational
226 stages but only on seedlings planted in gaps, but the trend was the opposite during summer,
227 when a higher probability of being browsed was observed for understory seedlings although
228 only in the subalpine stage (Figure 3). Finally, browsing rates on *P. sylvestris* were rather low,
229 and did not result in significant higher mortality rates at any environmental condition.

230 ### 3.3. Effect of microhabitat on browsing-induced mortality

231 The distance to the nearest shrub exerted a positive effect on the probability of mortality due to
232 browsing of *P. uncinata* and *A. alba* plants (Figure 4), meaning that a seedling planted further

from a shrub had greater chances of being browsed. For *A. alba*, this effect was modulated by elevation, and the response was higher at the subalpine belt, where the modeled probability of mortality increased from almost zero for a seedling growing at less than 50 cm from a shrub, to almost 1 for seedlings at more than 2.5 meters apart from a shrub (Figure 4). For *Betula* and *P. sylvestris*, the model that included distance to shrubs did not have stronger empirical support than the null model (Table 4), so an effect of distance to shrub on mortality for these species was discarded. This was also the case when the explanatory variables were herb abundance or light availability, and an effect of these variables on mortality could not be found for any of the species (data not shown).

4. DISCUSSION

4.1. Effects of micro- and mesohabitat on browsing patterns

We found both micro- and mesohabitat factors to exert a significant effect on browsing patterns and associated seedling mortality. At the microhabitat level we found, as expected, the browsing-induced mortality of *P. uncinata* and *A. alba* to decrease when seedlings were growing close to a shrub. The role of shrubs as facilitators of tree regeneration has been widely observed in mountain areas, where shrubs act as 'biotic refuges' for seedlings (Heuze et al., 2005; Milchunas, 2002; Vandenberghe, 2007). In Mediterranean mountains, habitat amelioration has been pointed out as the main mechanism behind this facilitative effect (Castro et al., 2004; Gómez-Aparicio and Canham, 2008). This was also observed in a previous work conducted in the same area, in which we found a protective role of shrubs on seedlings face to adverse climatic events (Ameztegui and Coll, 2013). The results of the present study indicate that, in addition to habitat amelioration, shrubs also increase plant survival by providing physical protection from herbivores, denoting that both mechanisms co-occur in Mediterranean mountain systems (as also found by Boulant et al., 2008). Contrary to some recent works conducted in other mountain systems (e.g. Häsler and Senn, 2012; Kupferschmid et al., 2013),

we did not find grass abundance to affect browsing probability in our study area. The high abundance of grasses present in all our plots is probably at the origin of this divergence.

Contrary to our hypotheses, the patterns of seedling consumption differed between summer and winter at the mesohabitat scale. During summer, *Betula* seedlings were heavily browsed in all conditions, whereas *P. uncinata* and *A. alba* were mostly browsed when growing in the forest understory. These areas are frequently visited by livestock, which commonly seek shade in the warmest hours of the day. They also have low shrub densities (especially in the subalpine belt), which results in a greater visibility of the plants and hence in a greater chance of being browsed. During winter, the opposite consumption pattern was found, and mortality associated to browsing was in general higher in plots located in gaps. The different duration of snow cover in the plots established in these areas might explain the observed patterns. Faster melting snowpack in gaps due to higher insolation can cause the seedlings to become available earlier in the year, during a period with potential scarcity of alternative food sources (Häsler and Senn, 2012; Jackson, 2009), hence increasing the pressure on them.

4.2. Impact of browsing on species-specific seedling mortality and forest dynamics

Browse-induced mortality rate during winter (i.e. caused exclusively by ungulates) was similar to browse-induced mortality observed during summer, when plots can be frequented by both wild ungulates and domestic cattle. However, intra-guild competition was probably occurring in the study area during summer, when the presence of forced the ungulates to take refuge in the rocky slopes located above the main grazing areas. Thus, assuming that most of the summer browsing-induced mortality is caused by livestock, our results indicate that livestock exert a lower browsing pressure than wild ungulates at current grazing conditions, as hypothesized. Livestock are usually characterized as ‘grazers’, since they tend to avoid the consumption of woody plants except in situations with very high stocking densities or fodder scarcity (Mayer, 2006; Vandenberghe, 2007). The high overall herb availability in the study area during summer

283 may thus have contributed to the moderate browsing pressure observed for livestock. On the
284 other hand, wild ungulates are more selective and cause more abundant and severe damages
285 than cattle to seedlings, often being described as 'browsers' (Didion et al., 2009; Liss, 1988;
286 Mayer, 2006, 2005b). The browsing behavior is particularly important during winter, when
287 other food resources are scarce and seedlings constitute a significant part of their diet (Häsler
288 and Senn, 2012; Jackson, 2009; Motta, 1996).

289 Herbivores showed a clear preference for birch seedlings throughout the whole study period,
290 both during winter and summer. Mortality values for *Betula* seedlings were much higher than
291 expected, since this species is not commonly considered as one of the preferred options of
292 browsers (see, for example, the reviews in Gill (1992) or Didion et al. (2011). The higher size
293 of birch plants compared to the other species could in part explain the observed differences,
294 since tall plants are browsed more often than smaller ones, the latter being often obscured by
295 surrounding vegetation or just ignored due to their small energy return (Kupferschmid et al.,
296 2013; Senn and Suter, 2003). In our study area, a positive relationship between seedling height
297 and the probability of being browsed was detected for our dataset when all species were
298 analyzed together (data not shown), but we could not detect this effect for any of the species
299 when analyzed separately, due to the small intraspecific variability in plant height.

300 For the three conifer species, browsing-induced mortality rates observed in the study area were
301 low or moderate, as they never exceeded 15%. The low browsing pressure observed on both
302 pines matches previous studies that suggest a low palatability of these species (Didion et al.,
303 2011). In contrast, fir is considered one of the preferred species by ungulates, which cause
304 significant difficulties for its regeneration in mountain areas of Central Europe (Ammer, 1996;
305 Heuze et al., 2005; Motta, 1996; Senn and Suter, 2003). In this study we unexpectedly found
306 low browsing rates on fir seedlings, but this could probably be explained by the small size
307 reached by the plants four years after planting.

For *A. alba*, *P. sylvestris* and *P. uncinata*, browsing induced similar or lower mortality than that observed for other causes, such as lack of climatic adaptation or sensitivity to extreme climatic events (Ameztegui and Coll, 2013). Therefore, one might conclude that browsing does not play a decisive role in the dynamics of these species, or at least not to the point of limiting or preventing their regeneration. For birch, which concentrated most of the damage by browsing, herbivory could be more limiting, especially considering the pioneer nature of this species, which normally regenerates abundantly in forest gaps after disturbances.

Although the mortality for the three conifers was not high, the lethality (i.e. the ratio of dead trees to damaged trees) was very high for all the species, and most seedlings died within a few months after being browsed. High lethality values associated to browsing are common at early life-stages (Senn and Suter, 2003), contrary to what occurs at more advanced stages, when mortality associated to browsing only happens in the most extreme cases (Häsler et al., 2008; Kupferschmid and Bugmann, 2013). In this study, 2-year old seedlings were planted at the limits of their distribution, and therefore at the limits of their physiological tolerance, as is apparent from their low growth rate and high mortality after adverse climatic events (Ameztegui and Coll, 2013). This may explain in part the high lethality we found given that the ability of plants to get over browsing is known to strongly depend on tree vigor (Kupferschmid et al., 2014, 2013).

4.3. Conclusions

The predation rate observed in this study was overall low or moderate, and should not represent a constraint for the regeneration of the study species. However, it is worth noting that this study focused on the first years of plant development, when plants are still relatively small. At higher plant developmental stages, more important browsing damages may occur, particularly if ungulate populations continue to grow favored by land-use changes.

Our results stressed important species-specific, seasonal, and habitat-related differences in plant damage by herbivores, which when occurred, was particularly lethal. The information derived from this study can be used by forest managers to adapt their practices and reduce browsing damages. For example, at the micro-habitat scale we showed that shrubs play an important role protecting seedlings from browsing. The known 'nursing' effect of shrubs has already been suggested as a technique to increase the success of reforestation plans in Mediterranean mountains (Castro et al., 2002; Gómez-Aparicio et al., 2008), and could also be used to promote species diversification of pine forests. Managers can control the understory shrubby vegetation through an adequate management of the canopy cover (Coll et al., 2010), seeking the conditions that minimize damages by herbivores. In a future context of increasing browsing pressure by wild herbivores, further knowledge in this topic may help foresters to define adequate forest management and planning strategies to allow regeneration success in these areas. Further studies might also be required to elucidate if the habitat-related consumption patterns observed in our study area are consistent across different forest types and browsing pressure gradients.

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466

FIGURE CAPTIONS

Figure 1. Location of the study area inside the (a) Iberian Peninsula; (b) the Pyrenees and (c) the Cadí-Moixerò Natural Park. Stars in (b) and (c) indicate the approximate location of the study plots.

Figure 2. Survival curves for seedlings of the four tree species planted at the two experimental sites over the course of the study period, based on Kaplan–Meier estimates of browsing-induced mortality. Black and grey lines represent seedlings in the montane and subalpine belts, respectively. Solid lines are Kaplan–Meier estimates whereas dashed lines are 95% confidence intervals. P-values indicate significance of the log-rank test between sites for each species. Shaded areas in the x-axis correspond to the growing season (from May to October). Note that the y-axis starts at 0. 4 for greater clarity and easier comparison among species.

Figure 3. Seasonal browsing-induced mortality (mean ± SE) for seedlings of *Abies alba*, *Betula pendula*, *Pinus sylvestris* and *Pinus uncinata* as a function of elevational belt (montane vs. subalpine) and type of cover (forest cover vs. gap). Asterisks above bars indicate values of mortality significant different from zero, whereas values above bars indicate the significance of the difference between mortality of seedlings growing under forest cover and gaps for a given species and elevation * P<0. 05; ** P < 0. 01; *** P < 0. 001. Values correspond to the mean at the end of the winter (month 32) and summer (month 39) periods.

Figure 4. Predicted variation in mortality risk for seedlings of *Abies alba*, *Betula pendula*, *Pinus sylvestris* and *Pinus uncinata* as a function of the distance to the nearest shrub. Black and grey lines represent seedlings in the montane and subalpine belts, respectively. Solid lines correspond to the predicted model, whereas dashed lines represent the interval defined by the parameter estimates ± 2 likelihood units. Horizontal lines indicate a lack of effect of the explanatory variable, and are only shown for comparative purposes.

TABLES

Table 1. Main abiotic and biotic characteristics of the studied stands at the meso-habitat and micro-habitat scale

	Montane site	Subalpine site
Meso-habitat variables		
Latitude (N) / Longitude (E)	42º19'/ 1º43'	42º18' / 1º42'
Elevation (m a. s. l.)	1550	1955
Aspect/Slope (degrees)	NE / 39	NE / 53
Bedrock	Limestone	Limestone
Mean rooting depth (cm)	57. 0 ± 9. 3	52. 5 ± 15. 5
Mean annual/summer temperature (ºC)	7. 4 / 14. 8	4. 9 / 11. 7
Total annual/summer precipitation (mm)	992 / 271	1118 / 327
Length of the growing season[1] (days)	194	147
Mean Summer Maximum Temperature (ºC)	21. 0	17. 3
Mean Winter Minimum Temperature (ºC)	-3. 4	-4. 6
Dominant species[2]	Ps, Pu, Bp	Pu, Aa, Bp
Main browsing period	June-September	
Livestock units[3]	124 (95 beef cattle + 60 horses)	
Micro-habitat variables		
Light availability (%PPFD)	19. 3 ± 9. 8 [2. 8-55. 1]	23. 9 ± 13. 3 [5. 4-58. 6]
Herbaceous Cover (%)	29. 2 ± 19. 8 [0-85]	43. 0 ± 29. 1 [0-100]
Distance to nearest shrub (cm)	59. 8 ± 52. 5 [10-400]	117. 5 ± 82. 2 [20-450]

Values for light availability, herbaceous cover, and distance to nearest shrub are mean ± SD.

Values in brackets are minimum and maximum observed values.

[1]Calculated as in Körner and Paulsen (2004)

[2] Listed for each site in decreasing order of dominance: Pu: *Pinus uncinata*; Aa: *Abies alba*; Ps: *Pinus sylvestris*; Bp: *Betula pendula.*

[3]Calculated as defined by the European Commission (http://epp. eurostat. ec. europa. eu/statistics_explained/index. php/Glossary:LSU)

501 **Table 2.** Observed mortality rates by apparent cause for seedlings of four species of trees
502 planted at montane and subalpine elevational belt

	Browse-induced mortality		Lack of adaptation		Random causes	
	Montane	Subalpine	Montane	Subalpine	Montane	Subalpine
Abies alba	0. 07	0. 13	0. 25	0. 11	0. 03	0. 15
Betula pendula	0. 42	0. 48	0. 15	0. 22	0. 03	0. 17
Pinus sylvestris	0. 08	0. 09	0. 24	0. 40	0. 04	0. 15
Pinus uncinata	0. 09	0. 07	0. 15	0. 13	0. 02	0. 20

503

504

505 **Table 3.** Observed browsing rate (percentage of browsed plants relative to the total number of
506 unprotected seedlings) and lethality (percentage of browsed seedlings that died within the next
507 months) for seedlings of four species of trees planted at montane and subalpine elevational belt,
508 and average for both elevations.

	Montane belt		Subalpine belt		Average	
	% Browsed seedlings	% Lethality	% Browsed seedlings	% Lethality	% Browsed seedlings	% Lethality
Abies alba	12. 5	77. 8	23. 6	70. 6	18. 1	73. 1
Betula pendula	65. 0	55. 6	63. 9	56. 5	69. 4	56. 0
Pinus sylvestris	11. 1	62. 5	18. 1	69. 2	14. 5	66. 7
Pinus uncinata	9. 8	85. 7	12. 5	77. 8	11. 1	81. 2

509

510 **Table 4.** Summary of the models predicting browsing-induced mortality as a function of micro-
511 habitat conditions for seedlings of four species of trees planted at two experimental sites in the
512 Eastern Pyrenees. For each species and explanatory variable, AIC of the best-fit model is
513 provided for all seedlings pooled together (AIC_P) and separated into two groups (montane vs.
514 subalpine, AIC_S).

Variable	Model	AIC_p	AIC_s	R^2
Abies alba				
Dist. to shrubs	Lin	78. 06	73. 91	0. 39
Null	Null	89. 85	83. 33	0. 13
Betula pendula				
Null	Null	52. 05	52. 51	0. 02
Pinus sylvestris				
Null	Null	59. 16	57. 76	0. 02
Pinus uncinata				
Dist. to shrubs	Power	52. 19	61. 10	0. 17
Null	Null	63. 37	63. 24	0. 03

515
516 For each species, only models with stronger empirical support than the null model (i. e. an
517 AIC_Pat least two units lower) are provided. Lower AIC_Svalues than AIC_Pvalues indicate
518 stronger empirical support for separated data than for pooled data, i. e. an elevational effect.
519 Models are: Lin = linear; Exp = exponential, Pow = power. Details on the model formulation,
520 parameter estimates and 2-units support intervals for the best-fit models are provided in
521 Appendix A.
522